

The use of aquatic plants by populations of the zebra mussel (*Dreissena polymorpha*) (Bivalvia: Dreissenidae) in a small glacial lake

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ABSTRACT

We examined the early life history of the zebra mussel (*Dreissena polymorpha*) in a small Pennsylvania lake with limited natural hard substrate. Veligers first appear in May, and settled on *Nuphar* (Yellow Water Lily) stems and concrete substrates in equal densities. Later cohorts, however, did not settle on the stems. Juveniles on stems abruptly abandoned their attachment in late August as the plant tissue began senescence. Aquarium experiments demonstrated that juveniles retained the ability to seek and find alternate substrates even after several months. Year-old zebra mussels were markedly unsuccessful in comparison. We speculate that in lakes with limited natural hard substrates aquatic plants may play an important role in zebra mussel recruitment, although juveniles must be able to locate alternate substrates as plant populations senesce at the end of the season. The resulting high mortality may limit mussel populations in these lakes.

Additional keywords: Invasions, substrate, life history, aquatic macrophytes

INTRODUCTION

Following the introduction of the zebra mussel (*Dreissena polymorpha*) to Lake St. Clair in the 1980s, much attention has been focused on the rapid dispersal and the environmental requirements of this invader (Griffiths et al. 1991, Strayer 1991, Hincks and Mackie 1997). Ludyanskiy et al. (1993) predicted that by the year 2000 the zebra mussel would inhabit all of North America's rivers, lakes, and reservoirs that fit within its broad range of ecological requirements. However, due to the limitations of overland dispersal the invasion of small inland lakes disconnected from navigable waters is taking much longer than initially anticipated (Kraft and Johnson 2000,

Bossenbroek et al. 2001). The glaciated portion of northwestern Pennsylvania, for example, has eight natural lakes all between 18 and 74 km from the south shore of Lake Erie, the most immediate source of veligers and adults, and all meeting the ecological requirements of *D. polymorpha*. To date, however, only two of them have established populations of *D. polymorpha* (Butkas and Ostrofsky, 2006) in spite of considerable recreational boat traffic among these inland lakes, and between these lakes and Lake Erie where *D. polymorpha* was first observed in 1989 (Griffiths et al. 1991). Observations from other inland lake districts in Illinois, Indiana, Michigan, New York, and Wisconsin have reported similarly slow dispersal and colonization (Miller and Haynes 1997, Kraft and Johnson 2000, Johnson et al. 2001). Consequently, the bulk of the published North American work on *D. polymorpha* has been from the Great Lakes and major river systems. The effects of this invader on small, inland lake ecosystems have received far less attention.

One of the characteristics of lakes in northwestern Pennsylvania and lakes in similar geographical settings is the relative paucity of natural hard substrates. These lakes tend to be small, with limited wind-generated wave energy to move fine sediments offshore. This combination of characters results in lakes with soft, muddy or peaty sediments right up to a shoreline that transitions through a zone of floating-leaved and emergent aquatic vascular plants. Rock outcrops and gravel bars are exceptionally rare. With the exception of the shells of native unionid mussels, the hard substrates that do exist are invariably man-made: docks, pilings, retaining walls, boat hulls, and waterlogged pieces of wood and other debris. Several studies have suggested that the colonization success and ultimate carrying capacity of *D. polymorpha* populations is determined by the availability of suitable hard substrates for attachment rather than by the quality and quantity of filterable food resources (Brady et al. 1995, Grigorovich and Babko 1997, Lewandowski 2001, Burlakova et al. 2006). There have been several studies that investigate the relative preferences displayed for

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substrate type, orientation, and texture by settling *D. polymorpha* veligers (Marsden and Lansky 2000, Kobak 2004, Czarnoleski, et al. 2004) but one possible substrate that has not received much attention is the surface of aquatic vascular plants (Lewandowski 2001). *Dreissena polymorpha* is known to attach to aquatic vascular plants (Horvath and Lamberti 1997, Diggins et al. 2004, Muskó and Bakó 2005). Hence, vascular plants may play an important role in the establishment and persistence of invasive populations in lakes with limited alternate hard substrates. However, while aquatic vascular plants offer considerable surface area, and often grow in dense stands that confer attached mussels some protection from predation by fish, they are seasonal and lack long term stability (Grigorovich and Babko 1997, Ozimek 1997). Most species rapidly senesce with the onset of cooler weather and shorter day lengths. To survive, attached biota must have the ability to abandon senescent plants and seek another, more permanent substrate.

In order to fully understand the ecology of the zebra mussel and the impacts it will cause as it continues to spread throughout North America, it is essential that we understand species interactions within small-lake ecosystems. In this study, we examined the early life history of a zebra mussel population in a small inland lake in Pennsylvania. We were particularly interested in the potential role of aquatic vegetation in a lake that otherwise provides few hard substrates. We sought to determine if aquatic plants could provide a substrate that was as acceptable to settling *D. polymorpha* veligers as more traditional hard substrates, and if, at the end of the vegetative growing season, settled juveniles retained the capacity to seek alternate substrates as the plant tissue senesced.

MATERIALS AND METHODS

All fieldwork was conducted in Sandy Lake, a small (~ 60 ha), moderately hard (total alkalinity ~ 70 mg/L) kettle lake located in Mercer County, Pennsylvania (41° 20.71' N, 80°06.43' W). Sandy Lake has a drainage basin area of only 7.2 km² consisting mostly of forest (52.6%) and low intensity agriculture (pasture/hay 39.7%, row crops 3.6%; USGS, 2000). Although no bathymetric map has been made to date, the maximum noted depth was 12 m. The lake stratifies from May through mid-October, with the thermocline at approximately 5 m. Hypolimnetic water below 9 m became anoxic by early July. Springtime total phosphorus concentration (~ 13 µg/L) and summer average Secchi disk visibility (3.5 m) suggest that the lake is oligo-mesotrophic (Ostrofsky, unpubl.). Sandy Lake is used primarily for fishing, swimming, and waterskiing. *Dreissena polymorpha* were first observed in the lake in 2000 (J. Widel, Lakeside Park Co., personal communication) and have been a conspicuous feature on hard surfaces ever since.

Water samples for the enumeration of planktonic veligers were collected weekly from three mid-lake locations

from mid-May to late-October 2004 (Figure 1). Two liters of epilimnetic water from each location were filtered through 0.45 µm membrane filters. Filters were dried, cleared with immersion oil, and mounted on slides. Veligers were identified using cross-polarized microscopy (Johnson 1995). Lengths of 200 (or n, if n < 200) veligers were measured to the nearest 10 µm using an ocular micrometer.

We monitored settlement of juvenile *D. polymorpha* on both artificial substrates and aquatic vascular plant surfaces. We used 0.093 m² concrete tiles (12"×12") placed in three lake locations (Figure 1) at a depth of approximately 1.5 meters. Tiles were put in the lake in May and retrieved in late August/September after veligers had disappeared from the water column. Juveniles found were preserved in 70% ethanol. The length of each juvenile was measured to the nearest 0.1 mm using a dissecting microscope and an ocular micrometer. We monitored the settlement of juvenile *D. polymorpha* on the submersed stems of the Yellow Water Lily *Nuphar variegata*. We collected ten individual stems (~0.75 m in length) from each of five macrophyte beds around the lake at weekly intervals from mid-May through September. Each stem was scraped to remove all attached organisms. All scrapings were preserved in 70% ethanol until examined. The total number of juveniles found on each stem was recorded. For each date sampled 200 (or n, if n < 200) juveniles were randomly selected and measured to the nearest 0.1 mm. Both veligers and settled juveniles were grouped into size classes and size-frequency graphs were constructed to estimate spawning and settling cohorts across the growing season.

To determine the ability of *D. polymorpha* to migrate to alternate substrates we suspended lake-collected macrophyte stems with 100 attached juvenile mussels in coarse mesh netting at the surface of each of 3 replicate 37 L (10 gal.) aquaria in the lab. The bottom of each aquarium was covered with a patchwork of unglazed ceramic tiles (15×15 cm) and fine lake sediments in a 1:1 substrate/sediment ratio. Each tank was filled with aerated lake water. After two weeks the macrophyte

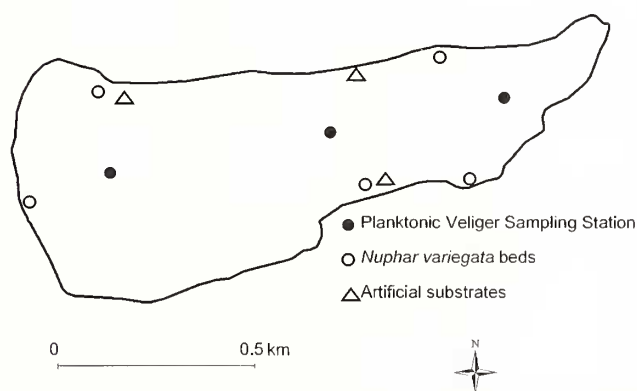


Figure 1. Map of Sandy Lake, Pennsylvania showing sampling locations for *Dreissena polymorpha* veligers, *Nuphar* beds, and artificial substrates.

stems had senesced, and stems, tiles, and sediments were examined for juveniles. We used χ^2 to test the null hypothesis of random settling (frequencies on tiles = frequencies on soft sediment).

To examine differences in the ability to seek and find new substrate as a function of mussel age, we established 8 replicate 37 L aquaria in the lab, each with fine lake sediment, aerated lake water, and a single tile giving a 1:5 tile to soft sediment ratio. To each aquarium we introduced 5 juvenile (6–11mm) and 5 adult (20–30 mm) *D. polymorpha* individuals to the soft sediment. Very few lake-collected mussels were found between 11 and 20 mm suggesting that these two size classes were from different spawning seasons. Tiles were examined daily and the number of juveniles and adults censused for 1 week. The rates at which juvenile vs. adult mussels accumulated on the tiles was taken as a measure of their ability to find alternate substrates.

RESULTS

Veligers were first observed in the plankton in late May when the epilimnetic water temperature was 21°C. There were no significant differences ($p > 0.05$, ANOVA) in veliger densities among the three lake sampling sites so data from all sites were pooled. Veliger density increased rapidly to a maximum of 17,500/m³ ($\pm 5,635$ s.e.) in late June, then rapidly decreased, disappearing from the plankton by early August (Figure 2). Measured veligers varied in length from 60 to 250 μ m, and size-frequency analysis (Figure 3) and changes in density suggest the presence of three cohorts: large ones in late May and late June, and a very much smaller one in late July.

Settled larvae first appeared on *Nuphar* stems in late June (Figure 4), reaching maximum densities in mid-July of 62 (± 20.7 s.e.) individuals per stem (approximately 1 individual/cm²). Settled juveniles showed a strong tendency to aggregate on a few stems rather than to accumulate evenly among all available stems. In 50% of the

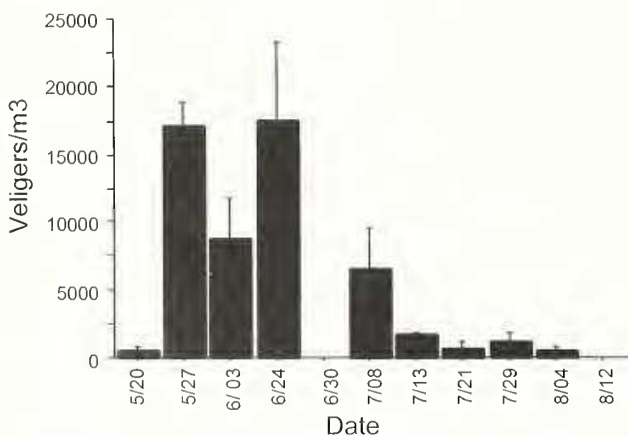


Figure 2. Mean *Dreissena polymorpha* veliger densities (± 1 std. error) in the epilimnion of Sandy Lake.

site x date collections the variance:mean ratio of settled juveniles on stems was significantly greater than one (χ^2 -test). The smallest measured juveniles were 200 μ m, approximately the same as the maximum veliger size in

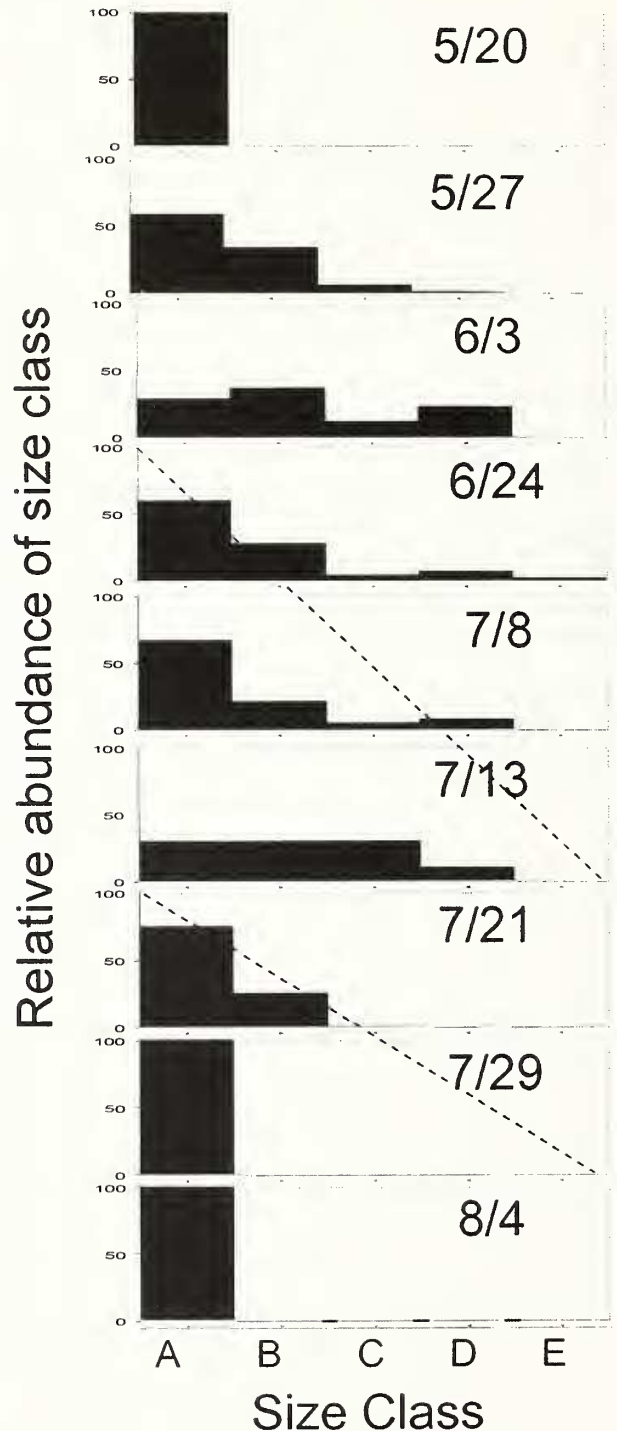


Figure 3. Size-frequency distribution of Sandy Lake *Dreissena polymorpha* veligers. Lines separate different cohorts suggested by both density and size distribution data. Size class A = <110 μ , B = 111–150 μ , C = 151–190 μ , D = 191–230 μ , E = >231 μ .

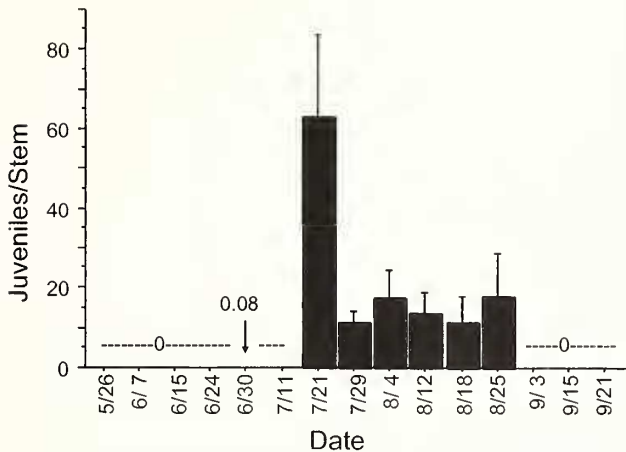


Figure 4. Mean density of juvenile *Dreissena polymorpha* (± 1 std. error) on stems of *Nuphar variegata* in Sandy Lake.

the plankton. Visual analysis of size-frequency data of the settled juveniles on stems (Figure 5) suggested only a single cohort with high initial mortality (77%) but very little mortality after late July. Juveniles abruptly disappeared from stems after late August. Adult *D. polymorpha* between 6 and 17 mm in length were occasionally observed attached to *Nuphar* stems, particularly early in the season. Individuals of this size were undoubtedly from the previous growing season. Concrete tiles collected at the end of the summer had densities of settled juveniles ranging from 0.11 to 2.69 individuals per cm^2 (mean = 1.0, s.e. = 0.9). There was no significant difference between the density of settled juveniles on concrete tiles and the maximum density measured on *Nuphar* stems ($p > 0.05$, t-test).

In the laboratory experiments approximately half (46%) of the juveniles on suspended vaseular plant stems in the aquaria abandoned their attachment sites within two weeks as the stem senesced (Table 1). We anticipated equal numbers would be recovered from the tiles and from soft sediments if displaced juveniles were incapable of migrating to firm substrates. We found that all of the displaced juveniles were recovered either on the tiles (26.7 ± 7.7 s.e.) or attached to the aquarium walls (19.0 ± 5.1 s.e.). None was recovered from the soft sediment. Those that remained attached to the plant material were assumed to be dead.

In the migration experiment comparing juveniles and adults, juveniles were found on the tile early and their numbers steadily increased (Figure 6). Adults appeared on the tiles late and in very small numbers. Rates of arrival on the hard substrate were 3.54 and 0.29 individuals/day for juveniles and adults, respectively. These rates were significantly different ($p < 0.05$, t-test for slopes).

DISCUSSION

An overview of the life history of *Dreissena polymorpha* given by Ludyanskiy et al. (1993) based largely on the

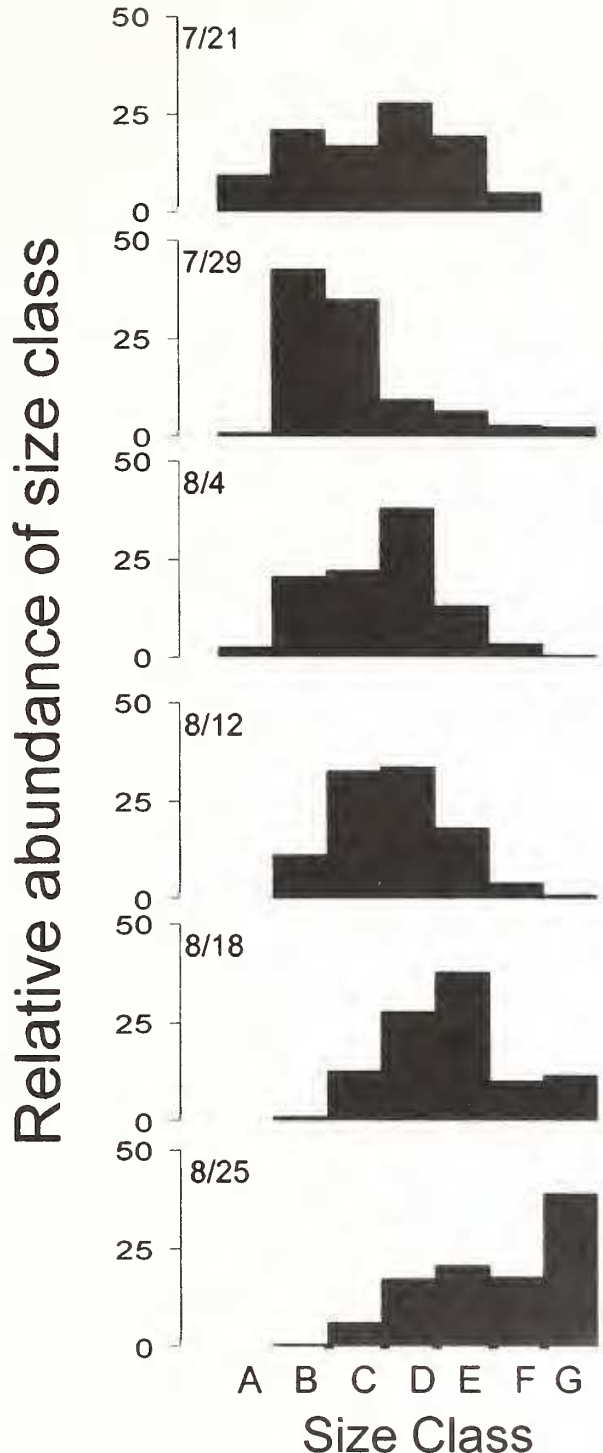


Figure 5. Size-frequency distribution of juveniles on *Nuphar variegata* stems. Data suggest a single cohort. Size class A = $<400 \mu$, B = $401-900 \mu$, C = $901-1400 \mu$, D = $1401-1900 \mu$, E = $1901-2400 \mu$, F = $2401-2900 \mu$, G = $>2901 \mu$.

European literature suggests that initial veliger size is about 70μ and that these veligers increase rapidly in size (up to 300μ) in 5 days to 5 weeks, at which time they can no longer remain suspended in the plankton and

Table 1. Distribution of juvenile mussels initially attached to senescing aquatic plants after two weeks. Approximately 46% of the mussels left the plants and successfully located an alternate hard substrate for reattachment. No mussels were found in the soft sediment.

	Tank 1	Tank 2	Tank 3
Initial # Mussels on Plants	100	100	100
No. Mussels on Tile	12	30	38
No. Mussels on Aquarium Wall	22	26	9
No. Mussels in Soft Sediment	0	0	0
Total Migrating	34	56	47
Remaining on Plants/Dead	66	44	53

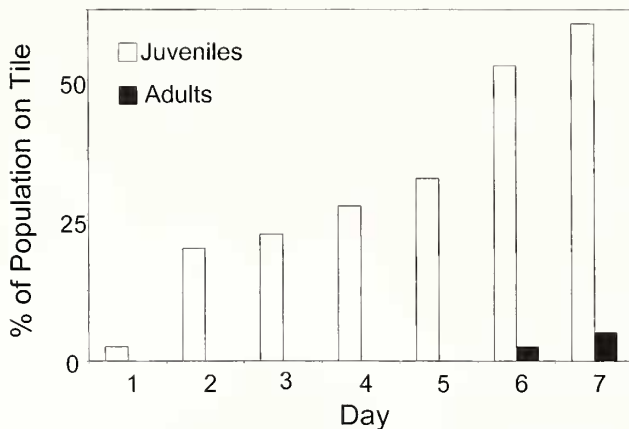


Figure 6. Migration of juvenile and adult *Dreissena polymorpha* from soft sediment to hard tile substrate in aquarium experiment.

settle on hard substrates. Veligers first appeared in Sandy Lake on May 20, and rapidly increased to a maximum density of about 17,500/m³. The smallest veligers were 60 μ m, and the largest were 250 μ m. We tentatively identified three cohorts based on size-frequency analysis.

The first juveniles appeared on *Nuphar* stems on June 30, and by July 21 had reached a mean density of 62 individuals/stem (approximately 1 individual/cm²). Size-frequency analysis of settled juveniles suggested only a single cohort (in contrast to possibly three veliger cohorts). Similarly, Wainman et al. (1996) found only a single three-week recruitment (settling) period in Lake Erie, also in July. We are confident that the first veliger cohort was the source of the settled juveniles because the smallest settled juveniles were approximately the same size as the largest of the veligers, and they overlapped temporally. The single cohort that successfully settled on *Nuphar* stems appeared to suffer high initial mortality, falling from a density of 62 individuals/stem to 11/stem in the first week. There was no further significant decrease in density until September 3, when densities fell to zero.

The abrupt loss of juveniles from plant stems at the end of August could be a consequence of increased predation—those on plant stems perhaps being particu-

larly vulnerable/visible/available—or could be the result of a mass abandonment of these attachment sites as a consequence of some perceived change in substrate quality. In late summer, *Nuphar* stems become heavily coated with epiphytic microorganisms, and the stems lose their firmness—either condition might signal a deterioration of substrate quality to the mussels. That *Nuphar* stems are attractive settlement sites early in the summer is supported by our observation that mean juvenile density on stems is no different from mean density on concrete artificial substrates collected at the end of the summer although the aggregated distribution on plant stems, and the data from the literature on other hard surfaces suggest that they are attracted by slight differences among otherwise similar surfaces or to each other (Wainman, et al. 1996). The lack of any evidence for the settlement of the second and third veliger cohorts on stems as the season progresses suggests that these sites become less attractive.

The fate of juveniles that abandon their attachment to *Nuphar* stems is unknown. Newly settled juveniles have the ability to seek alternate attachment sites by crawling or by using byssal threads to resuspend themselves in the water column and resettle elsewhere (Griffiths, et al. 1991, Marsden and Lansky 2000), and Martel (1993) has documented juveniles up to 2 mm in length in the plankton of Lake Erie under conditions of high waves and strong currents. Lewandowski (1982) has noted the presence of plant remains in the byssus of 1 and 2 year old individuals found in benthic colonies. We are aware of no studies that have directly observed the fate of established juveniles that have abandoned their attachment sites after several weeks, however. Juveniles leaving attachment sites at the end of the summer in Sandy Lake were large enough (77% were greater than 2 mm in length) that resuspension is an unlikely option. Juveniles may simply fall to the sediment surface and crawl seeking a better substrate.

The aquarium experiments did show that these large juveniles were capable of locating and successfully attaching to hard substrates after leaving senescing plant material. All of those that abandoned the plant stems in aquaria were found either on the tiles or on the aquarium walls. None was found on the soft sediments. This ability to find alternate substrates is lost with time, and year-old individuals were markedly unsuccessful compared to the younger cohort. At Sandy Lake we frequently encountered relatively large (6–17 mm) *D. polymorpha* individuals attached to plant stems or to the undersides of *Nuphar* leaves, particularly early in the season. We speculate that these individuals represent the previous year's cohort that abandoned plant stems, failed to find an alternate substrate, persisted on the surface of the plant litter in the littoral zone over the winter, then had a serendipitous encounter with an emerging *Nuphar* shoot the following spring. Lewandowski (1982) has also noted that 99.5% of the individuals found on plants are less than 0.5 mm in length, indicating that they belong to the youngest cohorts.

In Sandy Lake, and in other inland lakes with limited natural hard substrates it is likely that a significant portion of the annual *D. polymorpha* settlement occurs on plant surfaces – not only the relatively firm stems of *Nuphar* and emergent vegetation, but on the softer foliage of submersed plants as well. The available surface area provided by plants vastly exceeds that of alternate attachment sites. While the density of juvenile mussels on plants may be comparable to that on other substrates, mortality is considerably higher as a result of the need to abandon the plant surfaces with plant senescence, and the low probability of encountering an alternate site even though juveniles retain the ability to seek these sites. The resulting high mortality may be sufficient to limit the size of the adult population in lakes with limited hard substrate.

Why have zebra mussels failed to colonize small inland lakes in the midwestern US as anticipated by Ludyanskiy et al. (1993)? Johnson et al. (2001), noting low colonization success in spite of dispersal events estimated in the hundreds or thousands, cite three possible reasons for this failure. First overland transport is inefficient and many mussels attached to boats or to aquatic plants entangled in boats and trailers, or carried in bait wells or in bilge water fall off or die before reaching a new colonization site. Second, boaters do not visit lakes randomly, but rather visit a small subset of the most popular ones and long-distance dispersal fits a gravity model rather than a diffusion model (Bossenbroek, et al. 2001). Finally, overland transport and inoculation of new sites may occasionally be successful, but the colonists fail to found new populations. The causes of this failure are certainly varied. Butkas and Ostrofsky (2006) reported evidence of a failed introduction in Canadohta Lake likely due to too small an inoculum. Other introductions may fail as a result of inhospitable chemical or physical characteristics of the new site, including a paucity of favorable substrates for attachment. Lewandowski (2001) has estimated the survival of settling veligers to be usually less than 1%, and even in lakes with unusually well developed littoral zones less than 5% simply by failing to find an appropriate substrate. Further, those that do find substrates may not survive winter freezing or ice scour (Brady et al. 1995) if those substrates are in shallow water.

Our data suggest that the earliest cohort of settling veligers in Sandy Lake do not discriminate among substrates in that there was no significant difference between the density of juveniles on artificial hard substrates (concrete tiles) and their density on *Nuphar* stems. Karatayev et al. (1998) observed similar results in a number of European lakes when comparing juvenile mussel densities on a number of natural substrates including aquatic plants. Later cohorts in Sandy Lake did not settle on the stems, or settled on them in very much reduced numbers, evidently finding them less suitable than did the earlier cohort. Nevertheless, the surface area of plant tissue available for settlement greatly exceeds the area of other substrates (Brady et al. 1995,

Ozimek 1997), and Lewandowski (1982) estimated that more than 85% of the mussel population in 26 Masurian (Poland) lakes were using aquatic plants as substrates. However, the growing season of aquatic plants is shorter than the life of mussels, and on senescence mussels must abandon plant surfaces and seek alternate substrates if they are to survive. In Sandy Lake the density of juveniles on plants declined abruptly at the end of August. Lewandowski (2001) similarly found that populations of first year mussels on plants decreased by 78% between August and September in Lake Czoz due to plant senescence. Larger declines were seen in older mussels. Our laboratory experiments illustrate that these first year displaced mussels have the ability to migrate in search of alternate substrates, and our finding larger, second year old mussels occasionally on plant surfaces indicates that at least some are successful in that search. Lewandowski (1983) reported similar findings—that 2 to 3 year old mussels were found on plant surfaces in low numbers, 99.8% of the individuals were juveniles that had settled that year. However the cumulative effect of low settlement success and low survival of those settling on aquatic plants must severely limit the populations of zebra mussels in lakes lacking more permanent hard substrates.

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